ALARM RESPONSE OF THE INTERTIDAL SNAIL *LITTORINA LITTOREA* (L.) TO PREDATION BY THE CRAB *CARCINUS MAENAS* (L.)

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Many aquatic organisms rely on chemical senses to detect predators. Often avoidance behavior is elicited by distance or contact chemoreception of predator "odor" or "taste" (Mackie and Grant, 1974). Some species, however, have evolved alarm or escape responses to juices from the injured tissues of crushed conspecifics; these behaviors are found in minnows (von Frisch, 1938), amphibian tadpoles (Kulzer, 1954), sea urchins (Snyder and Snyder, 1970), sea anemones (Howe and Sheikh, 1975) and gastropod molluscs (Kempendorff, 1942; Snyder, 1967; Snyder and Snyder, 1971; Atema and Burd, 1975; Atema and Stenzler, 1977; Stenzler and Atema, 1977).

Snyder found in laboratory studies that 19 of 30 snail species tested respond to conspecific juice. He suggested that, in general, alarm reactions are responses to predation. Predators were tested for their ability to crush snails and elicit alarm responses in the laboratory. However, until Ashkenas and Atema (1978) reported that burrowing *Ilyanassa obsoleta* are rarely attacked by *Carcinus maenas* in the laboratory, no studies had tested whether responding with alarm behavior helps an individual snail avoid being eaten. Direct field observations of predation, which could support the antipredator hypothesis, have been lacking.

The present study was undertaken to test this antipredator interpretation. This paper describes the alarm response of *Littorina littorea* and field and laboratory observations of *Carcinus* predation on *L. littorea* and presents results of studies testing the utility of alarm behavior in preventing crab predation.

MATERIALS AND METHODS

Alarm behavior of Littorina littorea

Field experiments on the alarm repsonse of *L. littorea* were performed in tide pools of the rocky intertidal mid- and high zones at Bailey Island, Georgetown, and Harpswell, Maine. Snails found in small pools (< 25 cm deep, < 0.75 m² area) were tested in order to present snails with a high concentration of snail juice in tide-pool water. Snails responded to crushed conspecifics by moving to sites in the pool where they were less visible to a human observer. This response was measured by placing an octagonal grid (60 cm diameter, suspended from a circular plastic frame) over the tide-pool surface. Each trial lasted 60 min and consisted of a 30 min control period (min 0–min 30) followed by the experimental

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period (min 30–min 60).   At the beginning of the control period (min 0), two intact snails were dropped into the center of the grid area.   At min 30 (beginning of experimental period) two crushed snails were dropped into the center of the grid area (N = 6 trials).   The locations of snails visible under the grid were recorded at 10-min intervals for the full 60 min of each trial (after Atema and Burd, 1975).

Wet weight of snail tissue added to tide pools was determined by shell length–wet tissue weight regression.   Mean wet tissue weight of intact snails added to pools was 0.68 ± 0.07 g, N = 6 trials (in this and subsequent sections, values are reported as means ± one standard error).   Mean wet weight of crushed snail tissue added was 0.48 ± 0.20 g, N = 6 trials.   Fifty-nine ± 24.1 (range 17–122) snails were followed per trial.

A second experimental series was designed to test for responses to chemical stimulation by the snail juice alone.   At min 0 (beginning of control period) 6.25 ± 0.75 ml sea water was substituted for the intact snails of the first experimental series and at 30 min (beginning of experimental period) 5.45 ± 0.75 ml of filtered snail juice was substituted for the crushed snails (N = 4 trials). Snail juice was prepared at poolside just prior to each trial by crushing two individuals of *L. littorea* of known shell length (distance from apex to base of aperture) in a dish, adding sea water from another pool, and filtering the mixture through Whatman #1 filter paper into a 50 ml filtration flask.   Both sea-water control and snail juice were released from a pipette into the center of the grid area; again, each snail juice test followed a control trial.   Separate pipettes were used to avoid contamination between control and test stimuli.   The concentration of snail juice added was estimated by first determining the wet weight of crushed tissue from shell length–wet tissue weight regression.   The approximate concentration added was 0.12 g/ml of snail tissue in sea water before filtration and release into a tide pool.   In each trial 66.5 ± 33.3 snails (range 35–106) were followed.

In two additional blank trials the experiment was conducted in the same way but the test stimulus at min 30 was omitted.   In each trial 52 ± 36.9 snails (range 3–101) were followed.

To examine the rate of crawl of individual snails, in one Bailey Island pool 11 snails were marked individually with Pla enamel (Testors Corp., Rockford, Il.).   Positions of six individuals were recorded at 10-min intervals during a 30-min control (sea water) and a 30-min experimental test (filtered snail juice) period. This pool was tested on April 14 and May 3, but not every snail marked was present for both tests.   The movements of these individuals were also recorded during a 50-min blank trial on April 22 during which sea water, but not test stimulus, was added.

Predation by Carcinus maenas

To test the effectiveness of the *L. littorea* alarm response in preventing crab predation, the times required for crabs to find snails in "sheltered" and "exposed" sites were compared in the laboratory.   Also, the time required for snails to hide was compared to the duration of the "consume phase" of crab feeding behavior (Fig. 2).

The first comparison was simplified by using only one type of sheltered site chosen by snails in the field: a rock crevice.   Two round glass bowls (each 20 cm

diameter, 6.5 cm deep) filled with sea water to a depth of 6.0 cm were used to simulate tide-pool habitat. The bottoms of these bowls were lined with several flat rocks. Crabs were tested with "exposed" snails by placing snails in the center of a rock surface at one end of the bowl. In trials with "sheltered" snails, snails were placed in the approximately 2.0-cm-deep crevices formed between rocks.

Crabs used in these experiments were collected by commercial fishermen in Rhode Island, held in a damp refrigerated room for 3 days, and then transferred to two large (20- and 45-gal) aquaria in a recirculating sea-water system until experiments began 4 days later. Crabs were not fed during this time. Individuals of *L. littorea* were collected in Narragansett, Rhode Island, on the first day of the experiment and held in a damp glass bowl thereafter.

Crabs were placed in the bowls, allowed to acclimate for 10–30 min, then removed for 2–5 sec while a snail was positioned in the bowl. Both pools were used in "sheltered" and "exposed" trials. Between trials, pools were rinsed with hot water and refilled with fresh sea water. Distances between crab and snail were the same (approximately 16 cm) at the start of all 12 trials. The experiment took place in a dark room with the pools lit by a microscope illuminator. Crabs were observed for 20 min or until they had picked up a snail and moved it to the "attack" position in front of the mouthparts.

In a second experiment the time required for crabs to injure and consume snails was estimated using the same glass bowls. The goal of this test was to determine how long a crab takes to consume one snail before searching for the next, since this is the period of time available to intact conspecifics to find shelter. The "consume phase" of the predation sequence begins with first injury to the snail body and release of snail juice to the surrounding water. The exact time of first injury was difficult to determine, so this moment was standardized by equating it with a behavior involving sure injury, the "pull from mouthparts" (see below). The end of the "consume phase" was marked by completion of all feeding behavior. Each crab was placed with a small (< 9.0 mm shell length), medium-sized ($\geqslant 9.0$, $\leqslant 18.0$ mm), and large (> 18.0 mm) snail (Underwood, 1973) and observed until all the snails in the bowl were consumed or the crab showed no searching behavior for 10 min after consuming a snail.

Field observations of *Carcinus-Littorina* interactions took place in tide pools at Appledore Island, Maine. Feeding crabs were found at night by sweeping the red beam of a 9 V lantern (lens covered with a #2423 red plexiglas disc) over pool bottoms. Crabs were also observed feeding along the stony bottom of a cove at high tide during the day.

Results

Snail alarm behavior

The proportion of snails visible in the grid area decreased significantly in the 10 min period following addition of crushed snail ($P \leqslant 0.05$) or snail juice ($P \leqslant 0.025$) relative to changes in the proportion visible 10 min after introduction of intact snails or sea water (angular transformation of proportions; analysis of variance for paired data; Sokal and Rohlf, 1969). Snails tested in these trials hid by crawling into crevices, under fronds of macroalgae, or under rocks. In one pool, snails grazing at the tips of *Chondrus* blades moved down among the blades toward the holdfast. There was no significant change in the proportion of snails visible during the same intervals of blank trials (Fig. 1).
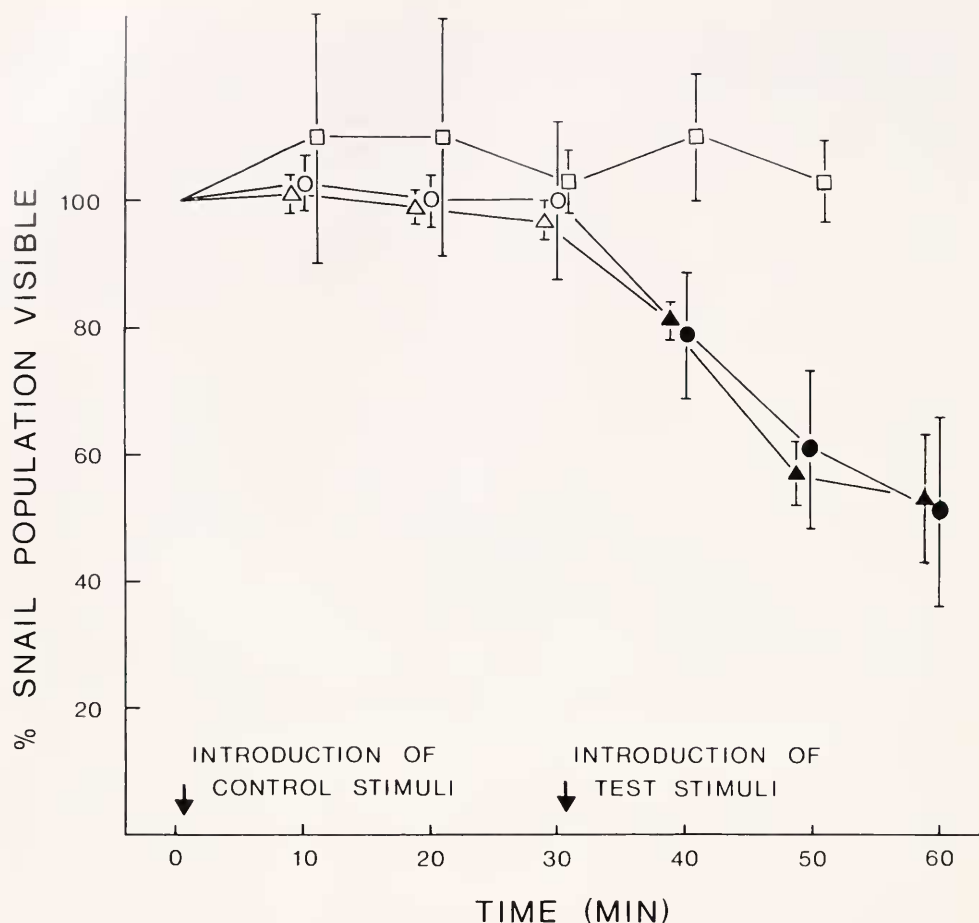
FIGURE 1. Percent of *L. littorea* populations visible following introduction of control and test stimuli, relative to percent visible at min 0. Stimuli introduced: open circle = intact *L. littorea* control; closed circle = crushed *L. littorea* (N = 6 trials). Open triangle = sea water control; closed triangle = crushed *L. littorea* juice (N = 4 trials). Open box indicates blank trials: intact snail or sea water was added at min 0 but no test stimulus was introduced (N = 2 trials). Symbols and bars represent means ± 1 standard error.

In general, snail activity in tide pools increased after addition of crushed snail or snail juice. Individuals in one pool increased rates of locomotion significantly, from 0.32 ± 0.07 cm/min (N = 6) in the 20-min interval preceding addition of snail juice to 1.40 ± 0.31 cm/min (N = 6) in the 20-min period following addition of juice ($P \leqslant 0.03$; Wilcoxon's signed-ranks test). In applying this statistical test, it was assumed that snails responded independently, although no experimental test for independent responses was conducted. There was no significant change in crawling velocity during the same periods of the blank trial.

Crab feeding behavior

Feeding crabs were observed in the laboratory and in the field. Detailed description of feeding behavior was based on laboratory observations.

Search phase. Feeding behavior begins when the crab detects, apparently by olfaction, the presence of nearby snails. First the antennule flicking rate increases (antennule beat, Fig. 2) and antennule position changes from primarily vertical to pointing at different angles from the carapace (antennule point, Fig. 2). The third maxillipeds then begin to sway from side to side and one may be wiped over the other several times. This may last for several minutes until the crab begins to move forward. The advance is accompanied by chelae and walking-leg raking, in which the chelae and walking legs are extended from the carapace and
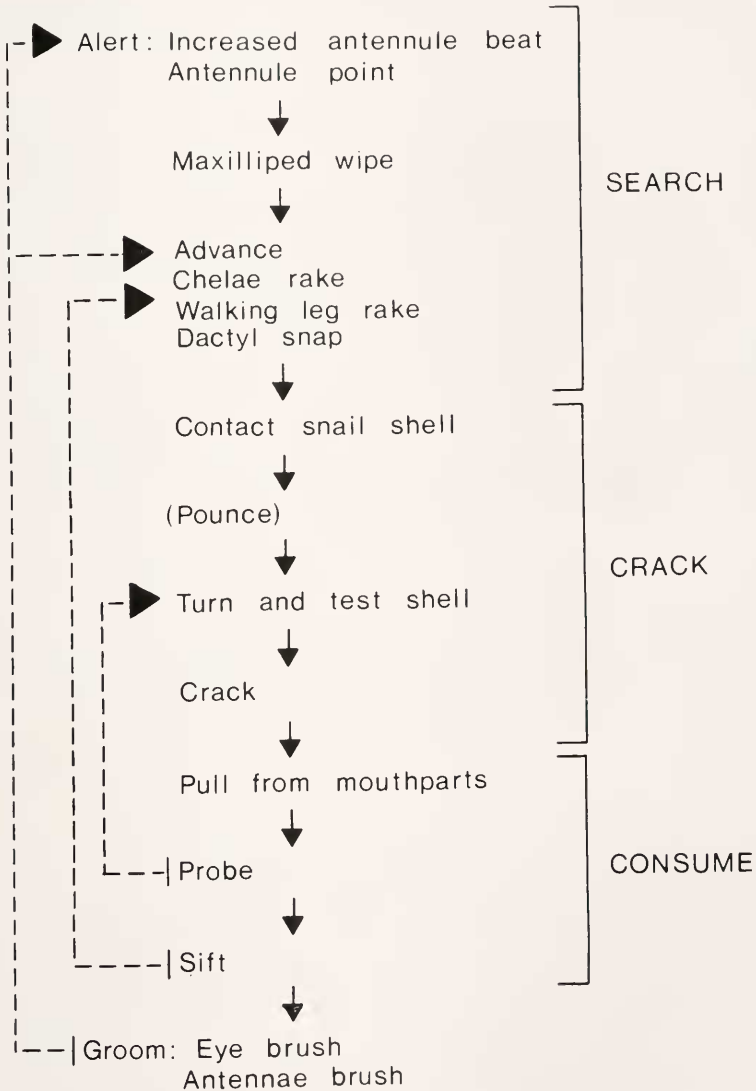

FIGURE 2. Sequence of crab (*Carcinus maenas*) predatory behavior. Dashed lines indicate points at which crabs may return to search or cracking behavior after having begun to consume a snail. This greatly lengthens the consume phase and increases the time available for intact snails to hide.

swept across the substratum with a semicircular swiping motion. While raking, the dactyl of the claw opens and closes (dactyl snap, Fig. 2).

Crack phase. Crabs begin their attack after contacting the snail shell with walking leg or claw. The crab may simply pull the snail from the substratum and bring it to the attack position in front of the mouthparts. Or the crab may suddenly pounce on the snail, pinning it between the carapace and substratum and then pushing the shell forward toward the mouthparts with the walking legs. Once the shell is in front of the mouthparts, the crab turns the shell over with the chelae, pausing to insert the dactyl of the claw into the shell aperture (probe, Fig. 2). The crab then removes the dactyl from the aperture and resumes turning the shell, stopping occasionally with one claw around the shell spire and the other supporting the shell. The third maxillipeds help support the shell during this turning and testing.

If the snail is small relative to crab size, the crab quickly crushes the shell with a claw or breaks off the top of the spire. If the shell is too large to crush, the crab uses alternative methods to expose the snail body; either chipping the outer lip of the aperture until the operculum is no longer flush against the shell and then grasping the snail body behind the operculum with one claw while the other claw tugs the shell in the opposite direction; or gradually chipping away the side of the shell. Either of these techniques requires further cracking of the shell after the first mouthful of snail tissue has been taken.

Consume phase. Once the snail body is exposed, the shell is held up to the mouthparts, supported by both chelae, and the mandibles and maxillipeds tear off bits of flesh. A small cloud of fluid appears around the mouthparts. While mouthparts grip the snail body, the shell is pulled away with the claws, exposing more snail body, until it is consumed. Occasionally the shell is dropped when the snail is only partially consumed but the crab is unable to crack more of the shell.

If the shell has been crushed or broken, the crab picks up the fragments again (sift, Fig. 2) after consuming the snail body. At the end of the "consume phase" the crab sits quietly, resumes searching, or grooms. A summary of the entire predation sequence appears in Figure 2.

In the field, crabs were usually discovered holding periwinkles in the "attack" position, but on one occasion the entire sequence of feeding behavior (search through consume) was observed in a tide pool.

Crab predation: laboratory experiments

Attention was focused on two periods of this predatory behavior to test the utility of snail alarm behavior in preventing crab predation. The two periods were the "search phase" (time between a crab's becoming alerted to the presence of a snail and its attack on the shell); and the "consume phase" (the interval between first injury to snail body and the start of a search for the next snail victim). If responding to snail juice helps snails avoid crab attack, then crabs should require more time to locate and attack sheltered than exposed snails. Also, the response time of snails to snail juice should be less than or equal to the duration of the "consume phase" of crab feeding behavior.

Crabs found and began attacking exposed snails in approximately 4 min, but required longer than 16 min to discover and begin attack on snails in crevices ($P \leqslant 0.005$, Wilcoxon two-sample test, Table I). Only three of six crabs tested

TABLE I

Results of tests comparing crab predation on L. littorea *in crevices or exposed on rock surfaces: Means ± one standard error. Crab size (carapace width in mm) exposed trials: 47.74 ± 1.15; sheltered trials: 47.44 ± 1.46. Snail size (shell length in mm) exposed: 9.83 ± 0.16; sheltered: 9.59 ± 0.19.*

Variable	Snail location		
	Exposed	Sheltered	
Time to crab alert (sec)	31 ± 14	25 ± 8	
range	(1–60)	(1–90)	
Time from crab alert to attack* (sec)	240 ± 79	972 ± 110	$P \leqslant 0.005$
range	(13–465)	(490–1199+)	

* Trial terminated at 20 min even if crab hadn't yet attacked.

with sheltered snails were able to find snails and attack within the 20 min limit of a trial. Crabs became alerted (signaled by antennule pointing) to snail presence equally quickly in both cases, but took longer or were unable to find sheltered snails. Also, once a crab's walking legs or claws had contacted snails in crevices, crabs seemed to have difficulty performing the claw movements required to extract snails from crevices. The time required to consume individuals of *L. littorea* depended on snail size (shell length). The regression equation relating snail size and time required to consume snails was: ln consume time = − 3.28 + 0.488 shell length, $R^2 = 0.40$, $N = 16$. Crabs took longer to consume medium-sized snails than small snails ($P \leqslant 0.05$, analysis of variance). This difference reflects different methods of attack on the two size classes of snail. All crabs consuming medium-sized snails interrupted actual feeding on snail tissue to resume attack on the shell. Small snails' shells were usually crushed immediately. Large snails were attacked (65%) but none consumed (Table II).

DISCUSSION

The size, shape, and structure of gastropod shells is often considered a snail's single or primary defense against shell-destroying predators such as birds, fish,

TABLE II

Crab predation success and the amount of time required to consume small, medium-sized, and large individuals of L. littorea.

	Snail size		
	Small	Medium	Large
Number of snails presented	17	17	17
Number (proportion) attacked	13 (0.76)	14 (0.82)	11 (0.65)
Number (proportion) consumed	8 (0.47)	8 (0.47)	0 (0.00)
Consumed snails			
Snail shell length (mm)	7.88 ± 0.20	10.53 ± 0.29	—
Crack phase duration (sec)	30 ± 6	1164 ± 442	—
range	(2– 45)	(25–3625)	
Consume phase duration (sec)	134 ± 52	594 ± 277	— $P \leqslant 0.05$
range	(15–480)	(163–2505)	

and decapod crustacea (Heller, 1976; Vermeij, 1974, 1976, 1978; Vermeij and Covich, 1978; Hughes and Elner, 1979; Zipser and Vermeij, 1978). In this paper I have assembled evidence for an alarm response of *L. littorea* and its function as a complementary antipredator device. To test the hypothesis that alarm behavior in this snail is an antipredator adaptation, answers to two questions were sought: Do crushing predators prey on *L. littorea* in the field? Is the snail's alarm behavior adapted to predator search and feeding behavior? Answers were derived from laboratory and field observations of crab predation, and from results of field studies of snail alarm behavior. Although further analysis of this behavior would require identification of the alarm substance, such tests were not included in this study.

Both direct and circumstantial evidence suggest that crabs feed on periwinkles in the field. *Carcinus* was observed eating *L. littorea* in tide pools and a stony-bottomed cove. The abundance of broken shells found with shell injuries matching shell damage known to have been inflicted by *Carcinus* in the laboratory suggests that crab predation is not a rare event.

Three characteristics of snail alarm behavior seem adapted to defense against the search and feeding behavior of *Carcinus*: the form of the alarm response, the means by which alarm is communicated, and the time taken by snails to hide.

Individuals of *L. littorea* responded to juices of crushed conspecifics by increasing crawl velocities and moving toward rock crevices and under macroalgae fronds. Thus, the result of alarm behavior is movement to sites where snails are less likely to be stumbled upon by crabs. A snail in a sheltered site is more likely to avoid detection or attack than a snail exposed on a rock surface (Vermeij, 1974) or on the tide pool floor. In the present study it was found that crabs required more time to find periwinkles in crevices and were less successful in attacking once these sheltered periwinkles were found. It is likely that sites under rocks provide a similar refuge.

The majority of gastropod species tested by Snyder (1967), including the mud snail *Ilyanassa obsoleta*, responded to conspecific juice with self-burial. In the laboratory, buried individuals of *I. obsoleta* were attacked by *Carcinus* less frequently than were mud snails exposed on the surface (Ashkenas and Atema, 1978). Responding to a chemical signal is adaptive in defense against activities of a nocturnal tide pool predators such as *Carcinus*.

It is not immediately obvious that a gastropod could avoid being consumed by simply crawling away from its predator or by moving to sheltered sites, since snails are notoriously slow creatures. The key to understanding why this strategy works is knowledge of the predator's feeding behavior and the type of refuge sought by snails. *Carcinus* uses different techniques to attack and devour bivalve and gastropod prey depending on prey size (Elner, 1978; Kitching *et al.*, 1966; Hughes and Elner, 1979; Zipser and Vermeij, 1978). The crab employed a similar size-specific strategy for *L. littorea*. Small periwinkles were crushed and consumed in 3 min, while cracking and eating medium-sized snails took about 26 min longer. Large snails were never successfully consumed in the laboratory. Thus, large individuals of *L. littorea* appear to have a size refuge like that reported for *I. obsoleta* (Ashkenas and Atema, 1978), *L. rudis*, and *L. nigrolineata* (Elner and Raffaelli, 1980).

Individuals of *L. littorea* found sheltered sites in approximately 10 min. Thus, the time required by snails to hide corresponded closely to the amount of time required by crabs to consume medium-sized snails, once first injury to snail

tissue had occurred. Although small snails are crushed and eaten too quickly to allow nearby conspecifics time to hide, with increased distance from the predator snails gain time to find shelter.

If the juice of crushed conspecifics signals a real threat to intact snails, crabs must search for a second snail after consuming the first (Snyder, 1967). All 11 crabs which consumed at least one *L. littorea* in the laboratory continued searching behavior after the first snail had been eaten. These crabs had been without food for 7–10 days when tested. In the field *Carcinus* probably feeds more frequently and may never consume more than one snail per feeding period. However, the single green crab observed through an entire episode of feeding in the field resumed searching as soon as the first snail was gone. Additional field observations are needed on this aspect of the snail alarm–crab predation relationship.

Of course, crabs are not the only predator of *Littorina* able to release snail juice. Carnivorous whelks (*Thais*), herring gulls, ducks, fish, and lobsters have also been reported to eat *L. littorea* (Pettitt, 1975). The shelter-seeking behavior of the snails may also be an effective defense against visual predators, such as birds. The alarm response would be equally effective against any predator which injures snail tissue, takes more time to consume a snail than snails require to hide, and consumes more than one snail per feeding period. However, the volume and mixing of water along the shore at high tide is so much greater than the volume and mixing in a tide pool at low tide that stimulus molecules probably do not reach concentrations sufficient to affect any snails but those a few millimeters from the crushed snail. Thus, alarm responses may only occur in tide pools or other areas where water is shallow and still, such as a tidal marsh at low tide.

In an evolutionary race between shell-crushing predators and their gastropod prey, the evolution of elaborate shell ornamentation, short shell spires, narrow opercula, or thick shell walls may be one line of defense for a snail (Vermeij, 1978). However, these morphological adaptations are more often found among tropical than among temperate species. It appears that a complementary first-line strategy for the temperate *L. littorea* is behavioral defense: alarm behavior which helps a snail avoid detection or attack. Perhaps the most interesting challenge remains: the unraveling of interactions among all selective pressures which together determine whether shell structure, alarm behavior, or a combination of the two evolves for snail defense.

SUMMARY

Individuals of *Littorina littorea* in rocky intertidal pools crawled to pool sites where they were less visible (into rock crevices; under rocks and macroalgal fronds) when either crushed conspecifics or juice from crushed conspecifics was added to

these pools. A significant proportion of snails hid in 10 min or less; individual snails in one pool tested quadrupled their crawling velocities after snail juice was added.

Field observations and laboratory experiments tested the hypothesis that this alarm behavior helps *L. littorea* avoid being eaten. Green crabs (*Carcinus maenas*) were observed consuming individuals of *L. littorea* in tide pools at night and along the shore at high tide during the day. In the laboratory, crabs required more time to locate and attack periwinkles in rock crevices than periwinkles on rock surfaces. The amount of time required to consume specimens of *L. littorea* depended on snail size (shell length), reflecting different methods of attack by crabs. Small snails (< 9.0 mm) were crushed, then consumed in approximately 2 min 30 sec. Crabs could not consume large snails (> 18.0 mm), but destroyed medium-sized snails ($\geqslant 9.0$, $\leqslant 18.0$ mm) by cracking the shell, tearing off bits of tissue, then resuming shell cracking to expose more snail tissue. This required a mean time of 9 min 54 sec once first injury to snail tissue had occurred, which approximately equals the 10-min response time of snails exposed to crushed snail or snail juice in the field. These findings indicate that the alarm response of *L. littorea* serves in defense against *Carcinus maenas*.

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